Quick guide

Stomatopods

Thomas W. Cronin

What is a stomatopod? Stomatopod crustaceans are commonly known as mantis shrimp, because their prey-catching (raptorial) appendages resemble those of praying mantises. They are strictly marine and are quite distinctive from all other crustaceans, having separated from them roughly 400 million years ago and having evolved on their own unique track ever since. About 500 species are recognized today, most living in shallow tropical waters on sand flats or in coral reefs. While unfamiliar to most people, mantis shrimps are actually very common in these habitats.

What's special about these mantis shrimps? Stomatopods are enchantingly destructive creatures. They actively hunt down and attack prey, using their mantis-like arms either as spears to snatch small invertebrates and fish from the water, or as clubs to bludgeon snails and small crustaceans to death. Because they tend to wipe out the animals in small, seawater aquaria within hours of their arrival, they are widely hated by aquarium hobbyists, who unwittingly import them in coral rock placed in the tank.

Most stomatopods are small, typically a few centimeters long, but some get to be the size of a lobster and can actually smash through the glass wall of an aquarium. Despite their pugilistic nature, mantis shrimps are quite attractive animals, colorfully marked and interesting to watch as they wander about, probing into cracks and crevices for potential food. Their compound eyes extend anteriorly on stalks, and the eyes are constantly in motion, giving mantis shrimps an air of inquisitiveness and intelligence. Being so unusual, mantis shrimps have been called 'shrimps from Mars', but they have also been likened to crustacean primates because of their behavior and their alert, active eyes.

With such amazing eyes, can stomatopods see color? Yes! Rather surprisingly, mantis shrimps have the greatest diversity of color receptor types known for any animal. Many species have ten different photoreceptor spectral classes that see in the human 'visible' spectrum (400 to 700 nm) plus another five or six types that operate in the ultraviolet. The color receptors differ in the visual pigments they contain, and some are spectrally tuned by colored filter pigments that overly each actual receptor.

Mantis shrimps have been trained to select an object of a particular color from an array of objects of different colors, demonstrating that they have true color vision and can therefore make discriminations based upon hue alone and not brightness. Oddly, the receptors that mediate color vision are aligned in a linear arrangement in the compound eye and thus sample only a thin strip of visual space. The rest of the visual field is apparently seen only in shades of brightness, so to fill in the missing color, the eyes must scan over objects of interest. To give a sense of the complexity of mantis shrimp color vision, humans have only four classes of photoreceptors, compared to the 15 or so of mantis shrimps, and only three of those are cone types used for color vision (the other is the rods, used in dim light).

What do these little animals do with such a complicated color vision? That is a good question. It is thought that complex color vision could be useful in the underwater environment, where contrast is low and anything that could be used to enhance the visibility of objects would be useful. Mantis shrimps do use a variety of color signals in their communication (that is why they are so colorful), but as color vision must evolve before color signals do, its original function was probably related to orientation and to finding prey.

For now, however, the explanation of stomatopod color vision remains speculative. We do hypothesize, though, that as their sense of color requires comparing a large diversity of spectral receptor inputs, it may be something like our auditory sense. Each receptor might signal the presence of a single color, much as the hair cells in the cochlea are specialized to signal stimulation by a single auditory frequency.

Any other oddities in their vision? You bet! Mantis shrimps have a diverse set of photoreceptors that visualize polarized light. Polarized light sensitivity seems exotic to us, but in fact it is widespread among arthropods and, indeed, other animals. We think that the polarization sense is used like the color sense for enhancing contrast underwater, making objects of interest easier to detect.

Stomatopods have done something quite unusual, however, in that they use biological polarizers as visual signals. Parts of the carapace of many species are structurally modified to reflect polarized light efficiently. The polarizers

Figure 1. A view of the stomatopod *Odontodactylus havanensis*, showing the large compound eyes and the mantis-like raptorial appendage.

are displayed prominently in intraspecific interactions, such as aggressive or mating behavior. These animals thus use patterns of polarized light in the same way that other species use color patterns, providing a unique and therefore unmistakable appearance to visual systems capable of analyzing polarization patterns. Also, since the polarization pattern is independent of the spectrum of illuminating light, the signal looks the same in a great variety of lighting conditions.

Is there anything else unusual about their visual signals?

Naturally — they seem to have discovered how to enhance their color signals by adding fluorescence. Water absorbs long-wavelength light (that is why it looks blue), so visual signals based on long-wavelength colors like yellow or red are not very useful at depths greater than 15 or 20 meters.

Some stomatopod species that inhabit these depths, however, still look yellow. They do this using fluorescence: light in the blue spectral range is absorbed by pigments that re-emit it in the greens and yellows.

Fluorescence allows animals like these to have a similar appearance over a large depth range, reflecting yellow light in shallow water and fluorescing it in deep. It is possible that fluorescent signals might be more common among aquatic animals than previously thought.

Where can I find out more about stomatopods and their vision?

Caldwell, R.L. and Dingle, H. (1976). Stomatopods. Sci. Am. *234*, 80–89.

Cronin, T.W. and Marshall, J. (2004). The unique visual world of mantis shrimps. In Complex Worlds From Simple Nervous Systems, F. Prete, ed. (Cambridge MA: MIT Press), pp. 239–268.

http://www.ucmp.berkeley.edu/aquarius/

Marshall, N.J., Jones, J.P., and Cronin, T.W. (1996). Behavioural evidence for color vision in stomatopod crustaceans. J. Comp. Physiol. A *179,* 473–481.

Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, Maryland 21250, USA.
E-mail: cronin@umbc.edu

Primer

Mosaic and regulative development: two faces of one coin

Peter A. Lawrence[1] **and Michael Levine**[2]

"*There seems to be no more a completely mosaic egg than a completely regulation one*" Waddington, Principles of Embryology 1956, Allen and Unwin, p63.

From the mid 1800s and for about a hundred years, mainstream embryologists ignored genetics and tried to understand the mechanisms of animal development without it. The attempt was a brave one, but it became increasingly foolish. In the early 20th century, the gifted embryologist Thomas Morgan realised the importance of genes and took what he thought would be a temporary diversion into genetics. But it was a long detour; only at the end of his life was he able to return to his beloved embryos. But most other embryologists continued to work as if genes were irrelevant (and some have carried on like this into modern times!). The most original and resourceful of the old school, such as Hans Driesch, Sven Hörstadius and Hans Spemann, approached embryos by transplanting or combining pieces. But many of their results were so counterintuitive and conflicting that their hypotheses became abstract and ornate. The philosophical and the whimsical found this attractive. By contrast, it was the mathematical and the rigorous who joined the new science of genetics. Naturally enough, the two types of scientist failed to understand each other and embryology drifted off into metaphysical swamps while genetics explored the dry savannahs of statistics. For lucid and entertaining insights into these times we recommend Klaus Sander's essays: "*Landmarks in Developmental Biology*".

Embryology developed a rich and impenetrable terminology. Some hypotheses were mutually exclusive and thus the terms came in opposing pairs. For example: the information needed to drive development could be either fully executed in the egg (preformation) or progressively elaborated from simpler beginnings (epigenesis); development could be driven by a vital force (entelechy) or by a chemical and structural process (an ontogenic machine); embryonic cells could be preprogrammed and have a limited fate (determined) or they could be unrestricted and able to contribute to any organ (totipotent); embryos could, as we discuss below, be either mosaic or regulative. Embryology courses and text books still feel it necessary to give students a sense of these debates, and we can understand this — we too grew up with them. However, there has been a revolution brought about by genetics and molecular biology and it is time to bury some of the old arguments. Here we look at the classification of embryos into those with 'mosaic' or 'regulative' development and ask if we should still preserve these concepts.

Mosaic and regulative embryos: the concepts

As students we were taught that embryos fall broadly into two classes: *Regulative* embryos were thought to be characteristic of the vertebrates. Regulation was defined by Driesch in 1909 as an embryo adapting to interference, such as removal of a part, by restitution to or towards the normal. In 1971, Sander argued that the concept of regulation should also encompass cases where parts of embryos respond to experiments by changing their fate away from the normal; it is the flexibility itself that is diagnostic, not the direction of any change. Intrinsic to the regulative process are interactions between embryonic